

Consequences of long-distance swimming and travel over deep-water pack ice for a female polar bear during a year of extreme sea ice retreat

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Abstract Polar bears (*Ursus maritimus*) prefer to live on Arctic sea ice but may swim between ice floes or between sea ice and land. Although anecdotal observations suggest that polar bears are capable of swimming long distances, no data have been available to describe in detail long distance swimming events or the physiological and reproductive consequences of such behavior. Between an initial capture in late August and a recapture in late October 2008, a radio-collared adult female polar bear in the Beaufort Sea made a continuous swim of 687 km over 9 days and then intermittently swam and walked on the sea ice surface an additional 1,800 km. Measures of movement rate, hourly activity, and subcutaneous and external temperature revealed distinct profiles of swimming and walking. Between captures, this polar bear lost 22% of her body mass and her yearling cub. The extraordinary long distance swimming ability of polar bears, which we confirm here, may help them cope with reduced Arctic sea ice. Our observation, however, indicates that long distance

swimming in Arctic waters, and travel over deep water pack ice, may result in high energetic costs and compromise reproductive fitness.

Keywords Climate change · Energetics · Long-distance swimming · Polar bear · Telemetry · *Ursus maritimus* · Sea ice

Introduction

Polar bears (*Ursus maritimus*) occur on Arctic sea ice where environmental conditions often preclude prolonged observations of individuals. Inference of environmental effects on polar bear behavior and body condition is generally made with semi-annual capture data from a sample of individuals within a population and course-grained spatial data (Regehr et al. 2006; Durner et al. 2009; Rode et al. 2010). Nonetheless, some observations which are not based on systematic surveys alert researchers and managers of phenomena that are potentially significant to the population (e.g., cannibalism; Amstrup et al. 2006). Anecdotal records of long-distance swimming by polar bears, for example, appear in the popular media but little quantitative data exists describing such movements and associated energetic costs. Long-distance swimming, likely represents a challenge to polar bear energy conservation and survival. Monnett and Gleason (2006) highlighted the dangers to polar bears undertaking long-distance swims and warned that continued extreme summer ice melts in the Arctic may lead to an increase in mortality from drowning. Sub-lethal impacts to polar bears engaged in long distance swimming, however, are not known.

In 2008, we initiated a study investigating fine-grain movement, activity and physiological responses of polar

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bears with the goal of understanding the costs and benefits of pack ice use versus land use by individuals during the ice minimum season in the Beaufort Sea. During this study, we observed a long distance swim and subsequent travel over sea ice by an adult female polar bear. The fine-grained resolution of our data allowed us to infer the impact of this behavior on the bear's energetics and reproduction. We describe the distance traveled, environmental conditions experienced, physiological responses, and associated costs to this bear, in terms of body mass and reproductive fitness. We relate our observations to established principles of energy conservation in mammals and energetic theory for terrestrial and aquatic locomotion in semi-aquatic mammals.

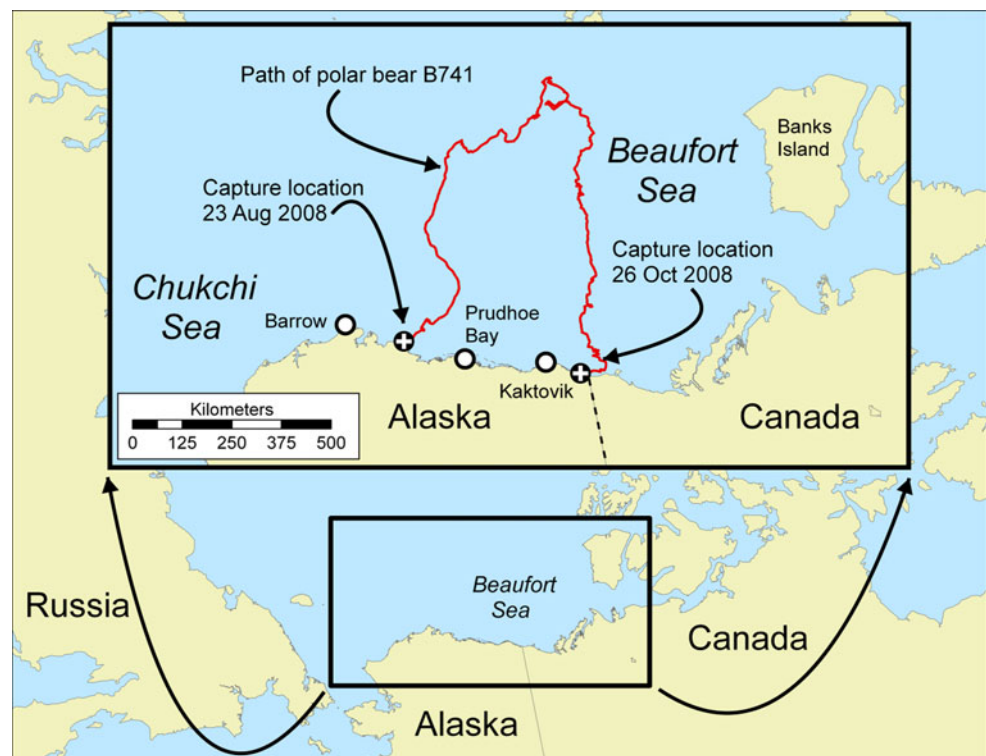
Methods

An adult female polar bear (hereafter referred to as 20741; estimated age 7 years by tooth cementum annuli; Calvert and Ramsay 1998) and her yearling female cub were captured on 23 August 2008 via helicopter darting (Stirling et al. 1989) on the Alaska Beaufort Sea coast (69.7188°N, 152.5621°W; Fig. 1). Bear 20741 was found alone and recaptured on 26 October 2008, near the Canada border (69.7291°N, 141.0938°W; Fig. 1). Bear 20741 was one of 29 and 20 polar bears captured in 2008 during August and October, respectively, on the Alaska Beaufort Sea coast, for research on the summer ecology of polar bears.

On her first capture 20741 was equipped with a GEN-III platform transmitter terminal (PTT) radio collar (Telonics, Mesa, AZ, USA) that included an on-board global positioning system (GPS) unit and an Argos ultra-high frequency (UHF) satellite uplink (Argos Data Collection and Location System, or ADCLS; Fancy et al. 1988). The collar stored hourly GPS location fixes during its deployment (i.e., 24 location fixes per day). Satellites uplinks occurred each day at 1000 Alaska Daylight Savings Time (ADST) for 4 h and sent the previous 6 GPS locations. While only 25% of the total daily GPS locations were transmitted through the Argos system, retrieval of the collar allowed the recovery of the complete history of GPS locations. This was because GEN-III radio collars are constructed with the UHF antenna located lateral to the neck of the animal; thus collar transmissions are impeded when the UHF antenna is submerged, as with a swimming polar bear. The GPS antenna, however, is located on the dorsal surface of the collar and GPS data was continuously collected as long as the swimming bear remained on the water surface. We calculated movement rate (km h^{-1}) as the distance traveled between hourly GPS locations, or the average distance if the duration between observations was >1 h.

Collar temperature (a proxy for ambient temperature) was measured hourly by a temperature sensor within the PTT. We also recorded activity with a 3-dimensional accelerometer (Mini-Mitter, Bend, OR, USA; Van Oort et al. 2004) attached to the belting of the collar. This sensor

Fig. 1 First (23 August 2008) and second (26 October 2008) capture locations (circles with white crosses) of adult female polar bear 20741 in northern Alaska. Also provided are place names indicated in the text and the complete travel route of 20741



provided a measure of activity that was independent of rate of travel estimated with GPS locations. Acceleration was sampled 32 times per second, and the greatest acceleration in each second was recorded as a unitless number. This “unitless number” was a measure relative to a baseline established by the sensor throughout the monitoring period (i.e., the time that the bear wore the radio collar). Every 10 min, measurements over the previous 2 min were summed to provide an activity “score”. We further averaged activity by hourly bins for reporting and analyses.

On the initial capture of 20741, a sterile temperature logger (accuracy 0.2°C, resolution 0.02°C, response time 5 min; Tidbit V2, Onset Computer Corporation, Pocasset, MA, USA), was surgically implanted slightly right and ventral of the base of the bear’s tail through a 5-cm incision. The logger, which was coated with inert wax (Paraffin Elvax, Respironics, Bend, OR, USA), was anchored to the surface of the *gluteus maximus* muscle beneath the subcutaneous fat with 0-gauge non-dissolvable suture (B. Braun, Bethlehem, PA, USA). The incision was stitched closed with the same material. The logger recorded subcutaneous rump temperature at 10 min intervals. Upon recapture of 20741, we removed the radio collar, activity monitor, and surgically retrieved the subcutaneous temperature logger. Average hourly collar temperature was used for reporting and analyses of ambient conditions.

We used several independent measures to assess travel and activity of 20741 between captures. Swimming bouts were first identified by an absence of received signals in the ADCLS data stream. Substrate occupied, (land, water, or sea ice) was determined by merging GPS locations with a landform GIS coverage and Advanced Microwave Scanning Radiometer for EOS (AMSR-E) imagery of sea ice concentration and extent (Spren et al. 2008). Differences in activity indices (i.e., activity counts, rate of movement, and distance traveled) and temperatures (i.e., rump temperature and collar temperature) were visually examined from the plotted data to identify major locomotion bouts, which we then statistically analyzed. Significant differences in mean activity and temperature indices (reported as the mean \pm 1 standard deviation, minimum, maximum, sample size) were compared among locomotion bouts with an ANOVA. Comparisons among locomotion bouts were performed with Tukey’s HSD test. Within bout trends (i.e., increasing or decreasing) of hourly activity and temperature measures were assessed with Pearson product-moment correlation (r_p). Correlations among activity and temperature indices were also determined with Pearson product-moment correlation. Statistical analyses were performed in SAS (version 9.1; SAS Institute Inc., Cary, NC, USA).

Sea state (i.e., wave height) and sea surface temperature (SST) were estimated from online data made available by Remote Sensing Systems (<http://www.remss.com>). Ocean

current speed and direction was estimated from data collected by 3 PTT buoys, which were provided by the University of Washington (<http://iabp.apl.washington.edu>). Ocean current speed and bearing were generalized with a second order polynomial applied to the buoy location data (Microsoft Excel 2007).

Results

Body mass at capture and recapture

Upon initial capture, 20741 and her yearling had body masses of 226 and 159 kg, respectively. Prior to our departure from the capture site, both bears were recovering normally from immobilization and no other polar bears or brown bears (*U. arctos*) were observed in the vicinity. Bear 20741 was not re-observed until her second capture on 26 October. During the second capture, the yearling was not present and researchers determined that 20741 was not lactating. At that time, 20741 had a body mass of 177 kg; a mass loss of 22% from that recorded on 23 August. When the capture team departed, 20741 was recovering normally from drug immobilization.

Estimating swimming bouts from ADCLS downloads

During the 3 days including and following the first capture of 20741 on 23 August the PTT successfully transmitted 13–20 messages per day to Argos satellites. GPS data received from ADCLS downloads indicated that the bear moved 1 km east of her capture location (70.8714°N, 152.5311°W). For comparison, during August 2008, 12 other polar bears were captured and equipped with PTTs. The median distance between their capture locations and their location on the third day following capture was 10.7 km. Three of these individuals traveled \leq 1.3 km from their capture location while the other 9 bears traveled up to 68.2 km. Between 26 August and 3 September, no PTT transmissions were received from 20741, and we assumed that the UHF antenna was submerged and that the bear was swimming. The resumption of satellite signal reception on 4 September with a location at 75.5231°N, 147.7668°W suggested that the bear had climbed to the surface of sea ice, exposing the UHF antenna and allowing successful transmissions to satellites. This location was a straight-line distance of >500 km north of 20741’s previous GPS location on land. AMSR-E imagery suggested that she swam for 9 days through an ice-free ocean. On 7 September there were no successful PTT transmissions, which again suggested that the bear was swimming. Successful PTT transmissions resumed on 8 September and occurred every day afterwards until 25 October (1–30 received

transmission per day), the day before 20741 was recaptured. The PTT signal reception history from 25 August–25 October (62 days) suggested that 20741 swam for 9 days, walked on sea ice for 3 days, spent another day swimming, and then walked on the surface of the sea ice for 49 days.

Estimating swimming bouts from the recovered collar and rump temperature logger

Recapture of 20741 allowed us to obtain the complete 2 month history of collar data and rump temperature data. Hourly location fixes were seldom absent and their frequency did not vary by mode of locomotion (duration between locations for swimming: 67.4 ± 27.8 min [min = 59; max = 300, $n = 228$]; duration between locations for walking: 67.5 ± 26.0 min [min = 58; max = 360, $n = 1081$]).

Patterns of GPS location fixes, movement rate, collar temperature, activity data, rump temperature, and sea ice imagery supported our interpretation of swimming and walking suggested by Argos transmissions. These data showed that the first bout of swimming began by 0600 ADST on 26 August 2008 and continued to 2200 ADST on 4 September, for a total of 232 h. As 20741 swam she traveled a northward curvilinear path of 687.1 km (Fig. 2a) at 3.0 ± 0.6 km hr^{-1} (min = 0.3, max = 4.3, $n = 228$; Fig. 3). Concurrently, activity score (1092.8 ± 344.3 , min = 284.2, max = 2114.5, $n = 233$) increased ($r_p = 0.79$, $P < 0.0001$; Fig. 3) and collar temperature ($5.3 \pm 1.1^\circ\text{C}$, min = 2.0, max = 7.0, $n = 228$) decreased ($r_p = -0.74$, $P < 0.0001$; Fig. 3) during the 9 day swim. Despite increased activity, subcutaneous rump temperature (mean = $32.3 \pm 2.2^\circ\text{C}$, min = 24.1, max = 35.6, $n = 233$) decreased ($r_p = 0.52$, $P < 0.0001$; Fig. 3). The decrease in subcutaneous temperature was correlated with a decrease in collar temperature ($r_p = 0.49$, $P < 0.0001$).

The resumption of Argos data and patterns of movement and sensor data suggested that the bear hauled-out on sea ice at 75.54703°N , 147.61086°W , at 2300 ADST on 4 September (Figs. 2b; 3). Sea ice at this location, however, was of such low concentration that it was below the detection capabilities of AMSR-E sensors, with the nearest measurable sea ice at 100 km to the northeast (Fig. 2b). Data suggested that the bear remained on sea ice until 2300 ADST 6 September. During this period 20741 traveled 68.6 km at 1.3 ± 0.4 km h^{-1} (min = 0.7, max = 2.8, $n = 44$). Both movement rate ($r_p = 0.58$, $P < 0.0001$) and activity score ($r_p = 0.47$, $P < 0.001$) increased during this time (Fig. 3). Collar temperature ($11.3 \pm 7.5^\circ\text{C}$, min = 2.0, max = 29.0, $n = 44$) and rump temperature ($36.4 \pm 1.3^\circ\text{C}$, min = 31.5, max = 38.9, $n = 49$) were higher than in the previous swimming period (Table 1), and were weakly correlated ($r_p = 0.31$, $P < 0.0001$).

Activity and movement rate were lower than in the previous locomotion bout (Table 1).

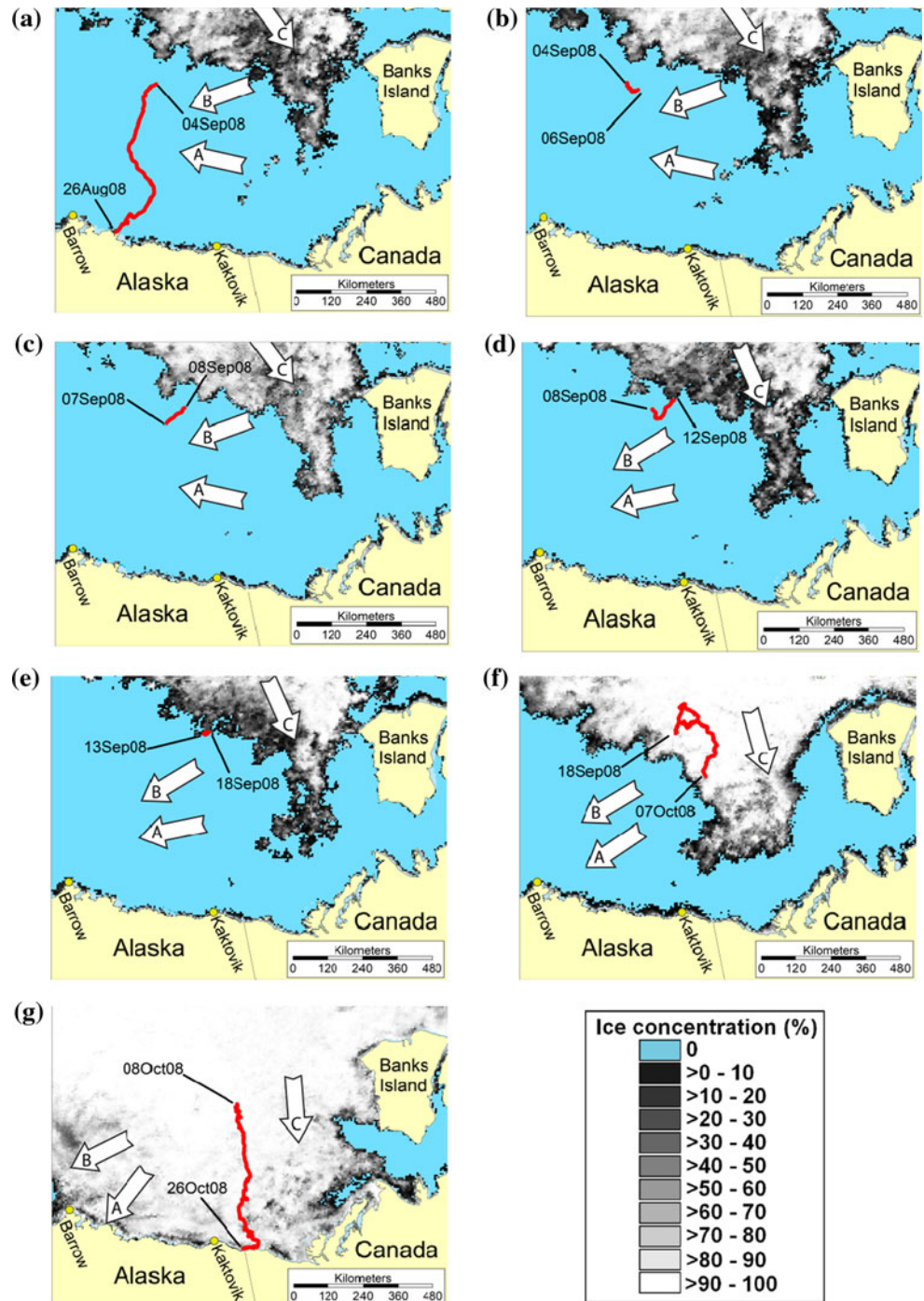
An absence of received Argos data between 0000 ADST 7 September and 0300 ADST 8 September, in concert with activity, collar and rump temperature data, suggested that 20741 reentered the water (Figs. 2c, 3). Recovered GPS and sensor data indicated that she swam 79.6 km (Fig. 2c). Movement rate (2.8 ± 0.3 km/h, min = 2.2, max = 3.5, $n = 28$) was greater than during the previous walking bout (Fig. 3; Table 1). Rump temperature ($32.8 \pm 1.3^\circ\text{C}$, min = 30.5, max = 35.4, $n = 28$) and collar temperature ($1.6 \pm 0.5^\circ\text{C}$, min = 1.0, max = 2.0, $n = 26$) declined during this swimming bout (rump temperature: $r_p = -0.90$, $P < 0.0001$; collar temperature: $r_p = -0.67$, $P < 0.001$; Fig. 3) and both averaged less than the previous walking bout (Table 1). Collar temperature was positively correlated with rump temperature ($r_p = 0.65$, $P < 0.001$).

On 0400 ADST 8 September the bear returned to the surface of apparently marginal sea ice (i.e., sea ice was below detection of AMSR-E sensors) and traveled 142.3 km to the northeast until 2300 ADST 12 September (Fig. 2d). Movement rate (1.2 ± 0.8 km h^{-1} , min = 0.1, max = 3.7, $n = 115$) and activity (491.2 ± 528.7 , min = 0.7, max = 1936.8, $n = 116$) were lower during this bout than during both swimming bouts (Fig. 3; Table 1). Collar temperature ($17.9 \pm 10.0^\circ\text{C}$, min = 1.0, max = 34.0, $n = 115$) and rump temperature ($36.7 \pm 1.2^\circ\text{C}$, min = 29.3, max = 38.3, $n = 116$) were greater than during swimming bouts (Table 1) and collar temperature was greater than it was during the first walking bout (Table 1).

From 0000 ADST 13 September to 0000 ADST 18 September bear 20741 was relatively sedentary. Although 20741 traveled 73.4 km, her straight-line displacement during these 5 days was only 10.8 km (Fig. 2e). Much of her track was convoluted and circled back over places previously visited. Her movement rate (0.6 ± 0.6 km h^{-1} , min = 0.0, max = 3.0, $n = 121$) was the lowest of all locomotion bouts (Table 1). Similarly, her activity (379.9 ± 547.5 , min = 0, max = 2103.0, $n = 121$) was lower than all locomotion bouts except the second walking bout (Fig. 3; Table 1). Collar temperature ($20.4 \pm 11.6^\circ\text{C}$, min = 0.0, max = 36.0, $n = 121$) was greater than all other bouts except for the second walking bout (Table 1). Rump temperature ($36.5 \pm 0.9^\circ\text{C}$, min = 32.8, max = 37.9, $n = 121$) was greater than during both swimming bouts and the last walking bout (Table 1). Rump temperature and collar temperature were negatively correlated ($r_p = -0.55$, $P < 0.0001$).

The final bout of travel, between 0100 ADST 18 September and 1300 ADST 24 October, included 1,413.9 km over sea ice (Fig. 2f, g). Movement rate (1.6 ± 1.3 km h^{-1} , min = 0.0, max = 5.5, $n = 870$) was similar to the

Fig. 2 Path of travel by a female polar bear in the Beaufort Sea, 26 August–26 October 2008. The data are binned by time periods of locomotion bouts and sea ice conditions (see text and Fig. 3): **a** 687 km swim, 26 Aug–4 Sep; **b** movement on marginal sea ice, 4–6 Sep; **c** 80 km swim, 7–8 Sep; **d** walking on marginal sea ice, 8–12 Sep; **e** resting, 13–18 Sep; **f** and **g** walking on sea ice, 18 Sep–26 Oct. Sea ice estimates are for the ending date of each panel (AMSR-E; Spreen et al. 2008). Approximate trajectories of 3 PTT buoys (A, B and C) are indicated by white arrows



first walking bout but greater than the second walking bout (Fig. 3; Table 1). Activity ($675.7 + 808.8$, $\min = 0.0$, $\max = 5841.0$, $n = 877$) did not differ from other walking bouts (Table 1). Collar temperature ($4.8 \pm 10.6^\circ\text{C}$, $\min = -12.0$, $\max = 34.0$, $n = 870$) was lower than in prior walking bouts and resting bouts but was similar to both swimming bouts (Table 1). Rump temperature ($35.2 \pm 3.0^\circ\text{C}$, $\min = 19.3$, $\max = 38.1$, $n = 877$) was

lower than the resting bout and other walking bouts but greater than each of the swimming bouts (Table 1).

Discussion

Polar bear 20741 demonstrated the extraordinary ability of this species to traverse great distances of ice-free ocean.

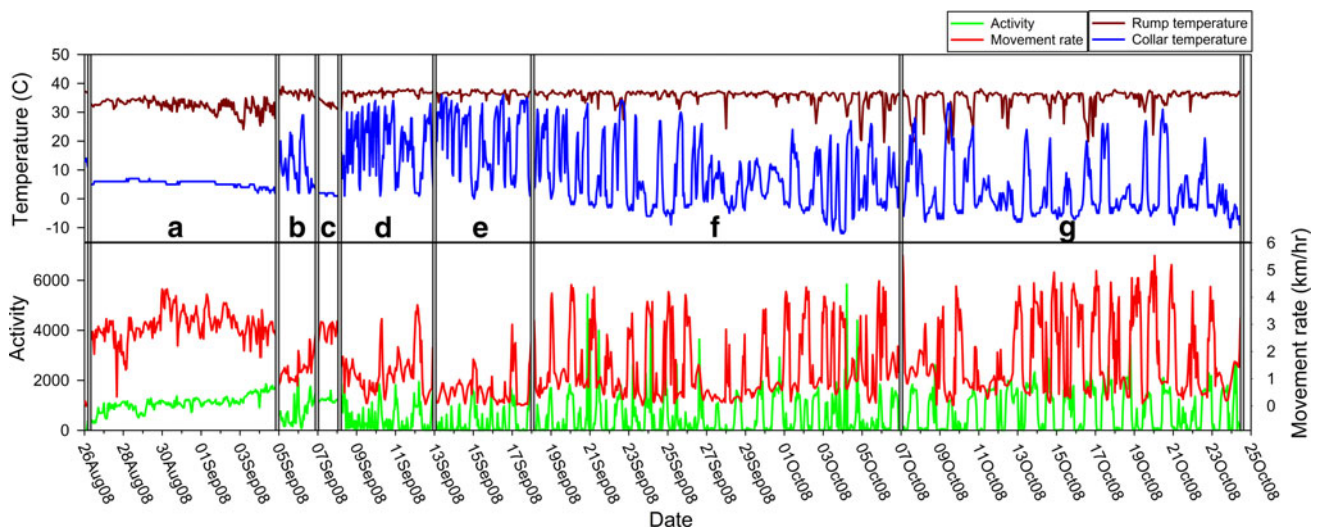


Fig. 3 Patterns of collar temperature, rump temperature, movement rate and activity for a female polar bear in the Beaufort Sea, 26 August–26 October 2008. The data are binned by time periods of locomotion bouts and sea ice conditions (see text and Fig. 3): **a** 650 km swim, 26 Aug–4 Sep; **b** movement on marginal sea ice, 4–6 Sep; **c** 80 km swim, 7–8 Sep; **d** walking on marginal sea ice, 8–12 Sep; **e** resting, 13–18 Sep; **f** and **g** walking on sea ice, 18 Sep–26 Oct

Table 1 Comparison of temperature and activity indices (ANOVA and Tukey’s HSD) relative to primary locomotion bout for a female polar bear in the Beaufort Sea, 26 Aug–26 Oct 2009

	walk1	swim2	walk2	rest	walk3
Activity, $F = 25.54_{[5,1418]}$, $P \leq 0.0001$					
swim1	↑		↑	↑	↑
walk1				↑	
swim2			↑	↑	↑
walk2					
rest1					↓
Rump temperature, $F = 75.78_{[5,1418]}$, $P \leq 0.0001$					
swim1	↓		↓	↓	↓
walk1		↑			↑
swim2			↓	↓	↓
walk2					↑
rest1					↑
Collar temperature, $F = 90.98_{[5,1398]}$, $P \leq 0.0001$					
swim1	↓		↓	↓	
walk1		↑	↓	↓	↑
swim2			↓	↓	
walk2					↑
rest1					↑
Movement rate, $F = 91.88_{[5,1398]}$, $P \leq 0.0001$					
swim1	↑		↑	↑	↑
walk1		↓		↑	
swim2			↑	↑	↑
walk2				↑	↓
rest1					↓

Tukey results indicate significant differences ($\alpha < 0.05$) of row values relative to column values. For example, Activity during locomotion bout swim1 was significantly greater (indicated by upward pointing arrow) than Activity during walk1, walk2, rest and walk3. Conversely, rump temperature was significantly lower in swim1 than during walk1, walk2, rest and walk3. Swim1: 24 Aug–4 Sep; walk1: 4–6 Sep; swim2: 7–8 Sep; walk2: 2–12 Sep; rest: 13–18 Sep; walk3: 18 Sep–26 Oct

Her long distance swim suggests that some polar bears prefer to remain on sea ice even when summertime ice extent is greatly reduced. Despite the ability of 20741 to complete this journey, the loss of 22% of her body mass could have compromised her subsequent survival and negatively affected her current reproductive effort.

The activity and temperature data that we collected from 20741 showed different signatures between swimming and walking. While 20741 swam her movement rate was relatively high and consistent compared to walking bouts. Levels of activity (as measured by the accelerometer) were also more uniform while swimming and did not display the daily peaks and troughs that were typical while the bear traveled on ice (Fig. 3). Although the rate of travel did not increase while 20741 swam, her activity level increased with time in water. Both rate of travel, activity, and collar temperature suggested that 20741 swam continuously for 9 days. In contrast to swimming, her activity on the pack ice varied greatly and likely included periods of rest as well as bouts with high activity (Fig. 3). Despite her constant activity while swimming, her subcutaneous rump temperature showed a chronic decline (Fig. 3). Subcutaneous adipose tissue can be an important insulator of body core temperature (Savastano et al. 2009). While an initial decline in rump temperature may have been due to shunting of blood away from peripheral tissues because of exposure to cold water (Rowell 1974), the chronic decline in rump temperature that we observed was likely caused by a decrease in thickness of the subcutaneous adipose layer (i.e., a loss of insulation) surrounding the logger (Savastano et al. 2009).

The survival of 20741 during her 9 day swim was likely influenced by sea conditions. Sea state was relatively calm (wind speed: 27 km h⁻¹) with waves 1–2 m in height (Bowditch 2002) during the time that the bear made her first swim of 687 km. In contrast, conditions preceding the observations of drowned polar bears made by Monnett and Gleason (2006) were severe, with near shore winds up to 54 km h⁻¹. Such wind speeds can produce waves exceeding 4 m in height (Bowditch 2002). Likewise, sea surface temperature (SST) was relatively warm (2–6°C) during the time that 20741 made her swim, compared to observations by Monnett and Gleason (2006) that drowned bears had been exposed to SSTs of 2°C. However, the exposure of 20741 to higher winds (36 km h⁻¹) and colder water temperatures (2°C) near the pack ice likely caused an increase in activity, which could have presented even greater challenges for thermoregulation near the end of her 9 day swim (Fig. 3).

A third factor that may have affected energetic demands while the bear swam north was that the general direction of ocean currents was largely perpendicular to her direction of travel (Fig. 2a). Speed and bearing of ocean currents

estimated from the location data of 2 floating buoys was 0.3 km h⁻¹ and 293° from true north (buoy A, Fig. 2a), and 0.1 km h⁻¹ and 253° from true north (buoy B, Fig. 2a). Conversely, her return to shelf waters in late September and October was likely assisted by the general speed and direction of currents pushing sea ice south through the eastern Beaufort Sea. Between 18 September and 26 October eastern Beaufort Sea ice movement was 0.4 km h⁻¹ at 188° from true north (buoy C, Fig. 2f, g). The general trajectory of ocean currents may have both hindered (swimming) and aided (walking) 20741.

In spite of the relatively benign environmental conditions during the time of the 9 day swim, the lower subcutaneous temperatures we measured for 20741 as she neared the pack ice suggest that chronic submergence may have lowered her body temperature and contributed to increased energetic demands. In general, mammals must maintain their body temperature within a narrow range to ensure normal biochemical and physiological functioning (Feldhamer et al. 2007). Some mammals tolerate substantial, regulated declines in body temperature during hibernation and dormancy (e.g. Lehmer and Biggins 2005), however, unregulated declines in body temperature due to environmental conditions can cause mammals to increase heat generation by elevating metabolic rate and, in turn, energy consumption (Maickel et al. 1967). It is noteworthy that in summer compared to winter, polar bear fur is thinner and provides less insulation (Frisch et al. 1974).

The choice made by 20741 to swim to the pack ice when the ice was >500 km north of the Alaska coast implies a preference of some polar bears for sea ice even when sea ice is at its annual minimum extent. Our observation is consistent with aerial survey data which has recorded a maximum of only 8% of the estimated 1,526 polar bears in southern Beaufort Sea (Regehr et al. 2006) remaining on land during summer (Schliebe et al. 2008). Swimming from land to ice floes, however, may be an adaptation for summers when sea ice persists within near shore waters and isolated floes are not far apart. During the late 1970s and throughout the 1980s, the summertime minimum sea ice extent remained within the near shore regions of the Alaska Beaufort Sea coast (Comiso 2002). However, in the following decade this same region experienced some of the greatest sea ice loss in the entire Arctic (Comiso 2002). We speculate that, until recent years of record ice retreat during summer, the choice to swim has not presented great risks to polar bears because swimming between land and pack ice would involve tens of kilometers instead of hundreds of kilometers. The current trend of reduced sea ice extent during summer, however, has moved the ice edge several hundred kilometers north, profoundly increasing the distance and assumed risks of swimming.

The body mass of both 20741 (226 kg) and her yearling (159 kg) appeared typical of female polar bears and their dependent young captured during August. Other captures in August 2008 and 2009 included four adult female bears with body masses between 220 and 315 kg and 6 yearlings with body masses that ranged between 149 to 199 kg. Bear 20741, however, lost more than a fifth (49 kg) of her body mass during the 65 days when she swam through open ocean and walked across the sea ice of the Beaufort Sea. Between 1982 and 2009, the mean body mass of 27 female polar bears with yearlings that were captured in October on sea ice or on land was 252 ± 44 kg (USGS, unpublished data). Of those, only two had a body mass <200 kg (i.e., 177 and 179 kg; similar to 177 kg of 20741). This may indicate that few female polar bears retain yearlings when their body mass is low, which further suggests that 20741's body mass was compromised by the end of her trek.

The rate of mass loss (0.75 kg day⁻¹) of 20741 was similar to the average mass loss (0.71 kg day⁻¹) experienced by pregnant polar bears in Hudson Bay (bears that are known to be food deprived) between the time they are forced ashore in summer to den emergence in the spring (Atkinson and Ramsay 1995). An important distinction between 20741 and Hudson Bay polar bears, however, is that traveling on pack ice may have provided opportunities to capture seals.

That this individual lost more than a fifth of her body mass despite spending about 1.5 months on the pack ice could possibly be explained by two scenarios. First, although polar bears are marine mammals in that they derive their nutrition from the sea they are not aquatic mammals. They are essentially a terrestrial mammal that lives on the surface of the sea ice. Swimming, when necessary, is accomplished through relatively inefficient alternate pectoral paddling (Fish 1996) with the hind limbs providing little or no forward propulsion. Even for a semi-aquatic mammal, such as mink (*Mustela vison*), the cost of swimming can be high relative to the cost of walking (Williams 1983). Although polar bears are good swimmers, their lack of a streamlined body shape and specialized swimming appendages likely contribute to a high cost while swimming. This, together with heat loss from submergence in cold water, possibly elevated energetic costs and resulted in the loss of body mass by this bear, even though she may have partially compensated for this by feeding on seals while later walking on the ice.

Alternatively, 20741 may have lost mass during both the long distance swimming event and the subsequent 6-week walking bout across the deep-water pack ice beyond the continental shelf and beyond areas frequented by seals. Throughout the Arctic Ocean polar bears prefer sea ice over the continental shelves (Durner et al. 2009) because the shelf seas have relatively higher biological productivity

than deep-water regions of the Arctic (Sakshaug 2003). Little is known about the distribution of Arctic seals during the season of minimum ice extent. As specialized benthic foragers, bearded seals (*Erignathus barbatus*; Burns 1981) rarely venture beyond the continental shelves. Ringed seals (*Phoca hispida*) often remain in the open ocean during summer (Harwood and Stirling 1992) and those that chose open ocean would not be available to polar bears on pack ice or land. Bear 20741, however, traveled for 53 days beyond the continental shelf (where water depth was >500 m deep). In fact, the average water depth at 1132 GPS locations beyond the shelf was 3409 ± 554 m. Based on our current understanding of the distribution of seals in the Arctic Ocean and the location record of bear 20741, it is likely that this bear had little opportunity to hunt seals during her trek across the pack ice to return to coastal Alaska. Certainly, the rate of mass loss experienced by 20741 is suggestive that she was food deprived. Thus, the combined long-distance swim and subsequent walk over the ice pack resulted in lower body weight of 20741 when she reached land.

The fate of 20741's yearling is unknown. Throughout the 40 year history of polar bear research in the Beaufort Sea, few independent yearlings have been observed (USGS, unpublished data), indicating that weaning after only 1 year rarely occurs. The only place where successful independent yearlings have been observed is in Western Hudson Bay (Derocher and Stirling 1995). It is possible that this yearling separated from her mother before the latter initiated her long-distance swim. It is more likely, however, that the yearling died during the long distance swim or subsequent walk. Mass-specific energetic costs of walking are greater for smaller than larger polar bears (Hurst et al. 1982). Likewise, mass-specific costs of swimming are generally greater for smaller versus larger animals (Fish and Baudinette 1999). Therefore, it would be reasonable to assume that this long-distance swim was more taxing for the yearling polar bear than for the adult and that the yearling succumbed to exhaustion at some point during the 9 day swim to the pack ice, or shortly thereafter.

Long distance swimming by polar bears may be a relatively rare event. Between 2004 and 2009 only 10 of 79 polar bears equipped with GPS collars in the Beaufort Sea have swam distances ≥ 200 km (USGS, unpublished data). However, our ability to identify swimming may be hindered by technological limitations. First, the full data from store-on-board GPS tags is available only if the collar is recovered. Second, the majority of collars deployed by the USGS were Doppler-type PTTs, whose temporal and spatial resolution is low relative to GPS technology and Doppler PTTs do not have store-on-board capability. Therefore, our ability to detect swimming by radio-tagged

polar bears may be possible only when the distance covered and the time spent swimming is great.

A potential concern of our observation is whether the behavior of 20741 might have been a response to handling. During August 2008, 12 other polar bears were captured on land and equipped with radio collars. Most of those individuals traveled greater distances than 20741 during the 3 days following capture, but 3 other bears had displacements similar to 20741. It may not be possible to reach a conclusion on a capture effect because the only aspect that distinguishes 20741 from other polar bears captured during that time was the long distance swim that began 3 days after her capture. Only one other bear captured in August 2008 made a long distance swim (113 km in 3 days) and that swim began 16 days following capture. During the prior 6 years several other long distance swimming events by polar bears have been observed (USGS, *unpublished data*), but they have lacked the detailed data that makes this account of 20741 so unique. These other swimming events were initiated >4 weeks following capture. While some bears swam from shore to sea ice, several bears embarked on long-distance swims from the pack ice to shore. Why some bears choose to swim to land or to the sea ice reflects an aspect of the individual variation among polar bears that is not yet understood. Regardless of their objective, this behavior can be costly when the distance is great and the conditions are potentially hazardous.

Our data from 20741 supports long-held assumptions drawn from anecdotal observations that polar bears are capable of prolonged swimming. Our data also suggests a preference of some polar bears for sea ice, even when that habitat is greatly reduced. Their ability to engage in long-distance swimming may help polar bears in a future of reduced Arctic sea ice. The high energetic and reproductive costs experienced by polar bear 20741, however, highlight the potential risks associated with long-distance swimming. Future losses of sea ice resulting from climate change may necessitate frequent long-distance swimming by polar bears. Associated declines in body mass and losses of dependent young may ultimately become an important mechanism for influencing population trends (Hunter et al. 2010; Regehr et al. 2010; Rode et al. 2010).

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